Reference: *Biol. Bull.* **182:** 1–7. (February, 1992)

# Fast-Strike Feeding Behavior in a Pteropod Mollusk, *Clione limacina* Phipps

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**Abstract.** High speed cinematography and video recordings were used to evaluate the fast-strike feeding response by which *Clione limacina* captures its prey, *Limacina helicina.* The acquisition phase of feeding involves rapid mouth opening and extrusion of three pairs of buccal cones. Mouth opening occurs in 10 to 20 ms, while hydrostatic inflation of the buccal cones takes 50 to 70 ms. Buccal cones are immediately retracted if prey are not contacted. Buccal cones surround the prey and release a viscous material that may be used as an adhesive attachment to the prey shell. Surface ultrastructure of the buccal cones reveals that they are studded with clusters of capitulate papillae, which appear to be the source of the viscous secretory material.

## Introduction

The pteropod mollusk *Clione limacina* feeds exclusively on shelled pteropods (Lalli and Gilmer, 1989). Due to the extremely limited dietary breadth of *Clione,* as well as the active swimming characteristics of both predator and prey (*Limacina helicina* in Friday Harbor, Washington), it is not surprising to find rapidly activated and highly specialized feeding structures in *Clione.* For prey acquisition, *Clione* rapidly extrudes three pairs of oral appendages, called buccal cones, which surround and adhere to the prey (see Lalli, 1970). Each buccal cone is cone shaped when retracted, but becomes more cylindrical when extruded. Extrusion of buccal cones is primarily due to hydraulic inflation (Lalli and Gilmer, 1989). The acquisition phase of feeding is followed by a manipulative phase, during which the prey is turned so that the shell opening is over the mouth of *Clione.* Manipulation is performed by the buccal cones and is followed by the consumptive phase, during which the prey is extricated from its shell. Extrication involves the use of two specialized hook sacs that form part of the buccal apparatus (Lalli, 1970). Each hook sac contains tufts of recurved chitinous hooks, which are protracted into the shell opening to grasp and pull the prey from its shell. Soft tissues of the prey are dislodged by alternate protractions and retractions of the hook sacs. Swallowing is aided by protraction and retraction movements of the radula, which is also part of the buccal apparatus. The soft tissues of the prey are swallowed whole (Wagner, 1885; Litvinova and Orlovsky, 1985; for other references see Lalli and Gilmer, 1989).

Two distinct forms of feeding behavior are observed. In the first, referred to here as the fast-strike response, *Clione* enters the acquisition phase of feeding from an unexcited, slow swimming activity state. During acquisition, swimming changes from slow to fast, and continues fast throughout the consummatory phase. During fast swimming, bending of the tail leads to frequent turning and looping movements of the entire body. If a fast-strike fails, and prey is not acquired, the buccal cones are immediately withdrawn, and fast swimming is terminated. The fast-strike response, which is initiated by prey contact, thus represents a sudden change to feeding behavior; if unsuccessful, the response is terminated by an equally sudden return to pre-strike swimming activity.

The second type of feeding behavior is initiated without direct physical contact with the prey. This activity involves fast swimming with loops and turns, as well as buccal cone extrusion and is referred to as "hunting behavior" (Litvinova and Orlovsky, 1985). Hunting behavior can be induced by placing an animal in seawater containing prey homogenates, by placing non-feeding *Clione* individuals close to feeding individuals, or by injecting sero-

Received 5 June 1991; accepted 25 November 1991.

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tonin into the hemocoel (Litvinova and Orlovsky, 1985; Kabotyanski and Sakharov, 1988). Hunting behavior is similar to fast-strike feeding behavior in that the mouth is held open with the buccal cones protruding, and swimming is fast with frequent changes in direction. The behaviors differ in two important ways. First, hunting behavior does not require direct contact with an intact prey. Second, buccal cone extension and fast swimming are maintained in hunting behavior, whereas both are terminated immediately in the fast-strike if a prey item is not acquired. Note that the prey acquisition responses of *Clione* form a continuum, with fast-strike feeding at one extreme and indefinite hunting behavior at the other.

In this paper, we describe behavioral and morphological aspects of the acquisition phase of fast-strike feeding; a cine analysis of mouth and buccal cone movements and a description of the surface morphology of the buccal cones are included. This work provides the background for an ongoing electrophysiological investigation into the acquisition phase of feeding behavior and the role of putative modulators on the motivational states underlying feeding behavior. It also extends the cinematic analysis of *Clione* feeding behavior by Litvinova and Orlovsky (1985).

## Materials and Methods

Both *Limacina* and *Clione* were collected from the breakwater at Friday Harbor Laboratories, Friday Harbor, Washington, and held in one-gallon glass jars in a seawater table. Individual animals were filmed in a small glass chamber filled with seawater at room temperature (16–18°C). Fast-strike sequences were filmed, within five days of animal collection, at 100 frames/s with a Redlake Locam high speed 16 mm camera containing Kodak Plus-X negative film. Additional feeding sequences were "filmed" with a Sony CCD video camera HVM-200, equipped with a Nikon Micro-Nikkor lens, at the equivalent of 60 frames/s and were recorded on a Canon VR-30 4-head portable video recorder. Feeding sequences were obtained by touching the prey, *Limacina helicina*, to swimming individuals of *Clione*. *Limacina* were attached with "Super Glue" to a human head hair or held in fine forceps.

A hair was attached to the *Limacina* shell as follows. A *Limacina* was placed in a shallow container on the stage of a dissecting microscope and the water level in the container was lowered until the shell, which is very hydrophobic, broke through the surface film of the water. The *Limacina* was then turned to achieve the desired orientation. The root of a human hair was quickly dipped in a small droplet of "super glue" and applied to the surface of the shell.

Fast-strike responses were recorded from five different individuals. One complete response (from initiation through acquisition) was recorded from each of these animals, but unsuccessful strikes were often recorded before the complete event. Unsuccessful strikes were also recorded from three other individuals that never produced a complete response. All animals were between 1.4 and 2.2 cm in body length.

Film sequences were analyzed frame-by-frame by making photographic prints of the sequences, and by projecting individual frames onto tracing paper. Tracings were made of body, wing, head, and buccal cone positions. In one case, the images from sequential frames were digitized from tracings with a Jandel Scientific digitizing pad and processed with a computer-assisted three-dimensional reconstruction software program, (PC3D™, Jandel Scientific, Corte Madera, California). Photographic prints were made by projecting 16-mm frames directly onto photographic paper with a standard photographic enlarger. Video sequences, advanced frame-by-frame, were traced directly from a television screen during viewing.

For scanning electron microscopical investigation, specimens that were not adhering to prey were anesthetized by immersion in a 1:1 solution of 0.33 *M* magnesium chloride and seawater. A *Clione* adhering to its prey was prepared as follows. First, a *Limacina*, glued to a hair, was dangled in an aquarium so as to contact swimming individuals of *Clione*. When one of the pteropods struck at and gripped the prey, it was immediately pulled out of the aquarium and dropped directly into the primary fixative solution. The specimen continued to grip its prey as they were both being fixed, and remained attached until $CO_2$ turbulence, during critical point drying, accidentally separated them, exposing the adherent surfaces. Fixation was completed by immersion in isotonic, cacodylate-buffered 2% glutaraldehyde, pH 7.3, at room temperature for 2 h, and postfixation was in cacodylate-buffered 1% osmium tetroxide for 1 h at room temperature. The specimens were dehydrated in ethanol, critical point dried from carbon dioxide, and sputter coated with gold and palladium before examination with an AMRay 1000 (Figs. 1, 4A) or a JEOL JSM-35 (Fig. 4B) scanning electron microscope.

## Results

### *Acquisition behavior*

Fast-strike feeding behavior was initiated by bringing a tethered *Limacina* into contact with the oral region of a freely swimming *Clione*. In our experience, the success rate of inducing fast-strikes was extremely low. With some animals, a day or more would pass without a strike being elicited; *Clione* apparently feeds irregularly. The degree of satiation in individual animals could not, therefore, be determined. The success rate was equally low, however, in animals that had been held in a jar for more than a week. With other animals, strikes could be obtained with some dependability. On one occasion, a response was obtained although the prey was not in contact with the oral region of *Clione*. In this case, the *Limacina* began rapid swimming movements when brought near the oral region of *Clione*, triggering an immediate fast-strike response.

In all observed fast-strike responses, the initial response of the acquisition phase was rapid mouth opening. When closed, the mouth forms a dorsoventral slit on the anterior margin of the head (Fig. 1A). Lip retraction pulls the lips laterally, causing mouth gaping and protrusion of the buccal cones (Fig. 1B). The degree of mouth opening can be judged from the position of the anterior tentacles, as recorded on film and video prior to and during fast-strike responses (Figs. 2, 3). The mouth of *Clione* is flanked by a pair of anterior tentacles that project from the anterolateral margins of the head (Fig. 1A). When *Clione* is hovering or slowly swimming forward (upward), the anterior tentacles are normally inflated and project forward (Figs. 1A, 2A). During mouth opening, lip retraction, and protrusion of the buccal cones, the anterior tentacles rotate laterally 90°, so that their projection is perpendicular to the longitudinal axis of the animal (Figs. 2D, 3). Mouth opening occurs in the first 20 ms of the fast-strike and is accompanied by full exposure and partial protraction of the buccal cones (Fig. 3). This can be demonstrated by pulling open the mouth of an anesthetized animal, which exposes the buccal cones and causes them to bulge slightly out of the mouth (similar to that seen in Fig. 1B). Three buccal cones lie on either side of the buccal mass (a muscular organ containing the radula and a pair or hook sacs), in a line parallel to the lips. The retracted cones are not inverted, but rather are collapsed and retracted into small cavities, or cheek pouches, adjacent to the buccal mass. Buccal cones protract when they are inflated with hemolymph (Lalli and Gilmer, 1989). This is supported by our physiological experiments in which induced activity in buccal cone protraction motor neurons causes mouth opening, contraction of head musculature, but only partial extension of buccal cones (Norekian and Satterlie, in prep.). In these preparations, full expansion of the buccal cones is impossible because the head hemocoel is compromised to allow electrophysiological recordings. In intact animals, expanded cones can extend approximately one-half body length from the mouth. Expansion is accompanied by a decrease in the diameter of the head and the appearance of a distinct circular constriction in the neck region (Figs. 2D, 3). In two recorded sequences in which the head and neck outlines were clearly shown, the reduction in head diameter averaged 22.7% while the reduction in neck diameter averaged 20.2%. Full expansion of the buccal cones, including the initial mouth opening, takes from 50 to 70 ms (Fig. 3). If the prey is not contacted during buccal cone expansion, the cones are immediately retracted, the mouth is closed, and the animal returns to slow swimming. Retraction of buccal cones is not a passive deflation, because the cones can be fully retracted in 70 to 90 ms (based on three unsuccessful strikes). On two occasions, strikes were aborted when the buccal cones were inflated to only 10 to 20% of the body length. In these cases, the cones were immediately retracted as in unsuccessful strikes.

Inflation of the buccal cones occurs from the base outward; the tips of the cones do not inflate until late in cone expansion. The uninflated tips are more opaque than the inflated parts of the buccal cones (Fig. 2D). As the cones

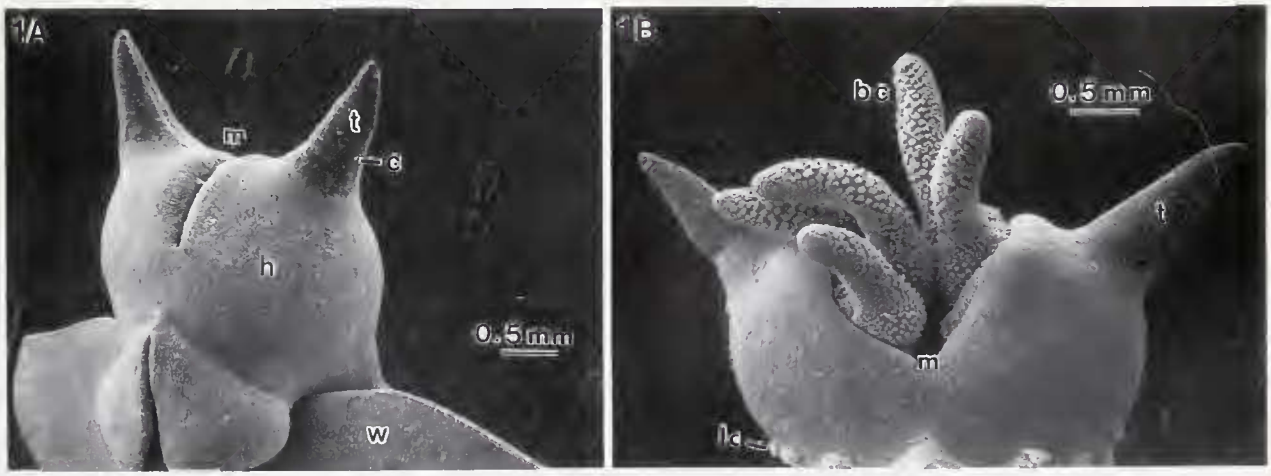

**Figure 1.** Scanning electron micrographs showing ventral views of heads of *Clione* in normal swimming posture (1A) and with mouth (m) open and five of six buccal cones (bc) partially protruded (1B). Note the pair of anterior tentacles (t) that bear ciliary tufts (c). The head (h) is covered with a coat of motile cilia. w—wings, lc—tufts of large neck cilia.

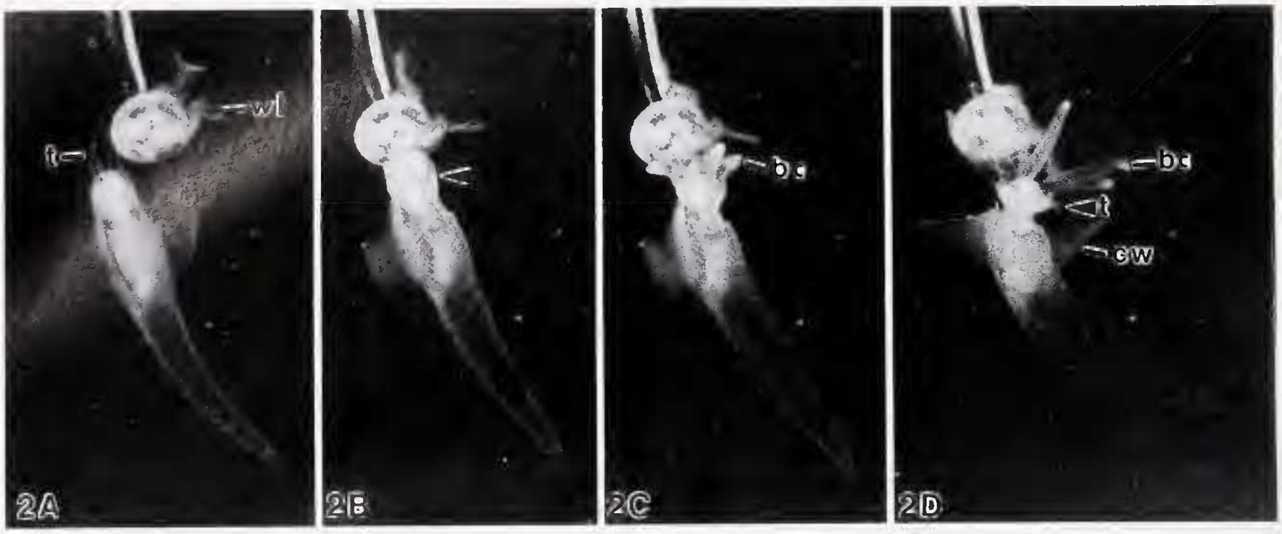

**Figure 2.** Representative frames from cinematographic series taken at 100 frames/s showing a tethered *Limacina* being offered to a *Clione*. cw—wings of *Clione*, wl—wings of *Limacina*, bc—buccal cones, t—anterior tentacles of *Clione*. (A) Predator and prey 200 ms (20 frames) before first sign of response to contact. (B) First sign of response to contact. Note the slight bulge on head of *Clione* (arrow). (C) Next frame (10 ms) after (B), showing buccal cones exploding from cheek pouches and forming grasping tentacles. (D) 4 frames (40 ms) after (C), showing buccal cones near full extension and beginning to grip the *Limacina*. Note the decreased diameter of the head, and the prominent neck constriction.

are extruded, they project outward at approximately 45° with a slight concave curvature with respect to the mouth. As the cones reach full expansion, they bend around the prey and adhere to its shell (Fig. 3).

*Limacina* shells pulled from the grasp of *Clione* buccal cones were coated with a viscous residue in the regions contacted by buccal cones. Clear viscous material produced by the buccal cones could be gripped with fine forceps and lifted in fine strands from the surface of the seawater containing the *Clione*. During hunting behavior, the protracted buccal cones frequently adhered to the wall of the container following contact with it. Removal of an adhering animal revealed residue on the glass, apparently adhesive.

### *Surface ultrastructure of the buccal cones*

The surface of each buccal cone is studded with clusters or rosettes of capitulate papillae (Fig. 4). The number of papillae in each cluster varies from two or three to about a dozen. The clusters near the bases of the buccal cones contain the fewest papillae per rosette, those toward the tips contain more. Each papilla is about 15 $\mu$m high and somewhat less than 10 $\mu$m in diameter. The tip of each papilla is slightly inflated, forming a lumpy capitulum about 10 $\mu$m in diameter. Each rosette has a common stalk, about 20 $\mu$m in diameter and 20 $\mu$m in height. Long cilia protrude from the sides of the papillae and project from the surface of the buccal cone between the papillae. Tight clusters of cilia protrude from the centers of some of the papillary rosettes. Isolated clusters of cilia, were also observed, but they were not common (Fig. 4A).

When the buccal cones are retracted, the epidermis between the clusters of papillae is deeply folded, and the capitula and cilia form a tightly packed feltwork or welter on the surface of each cone. When the buccal cones are extended, the rosettes of papillae stand up above a smooth, simple squamous epithelium that stretches tightly over the tentacular surface between the rosettes of papillae (Fig. 4A).

The surface of the shell of *Limacina*, to which the buccal cones adhere, is very smooth, transparent, and very hydrophobic; it appears smooth when viewed with a scanning electron microscope. The shells of dead *Limacina* lose their hydrophobic properties rapidly. Where the shell of a *Limacina* is contacted by the buccal cones of a fast-striking *Clione* are fine threads, observable by SEM, that correspond to those that appear on the surfaces of the buccal cones where they contact the *Limacina* shell (Fig. 4B). These threads appear to originate from the tips of the capitulate papillae, but this possibility is difficult to establish with certainty.

## Discussion

The fast-strike response of *Clione* consists of a rapid opening of the mouth and a hydraulic inflation of the six buccal cones, the entire response occurring in 50 to 70 ms. In aborted or unsuccessful strikes, withdrawal of buc-

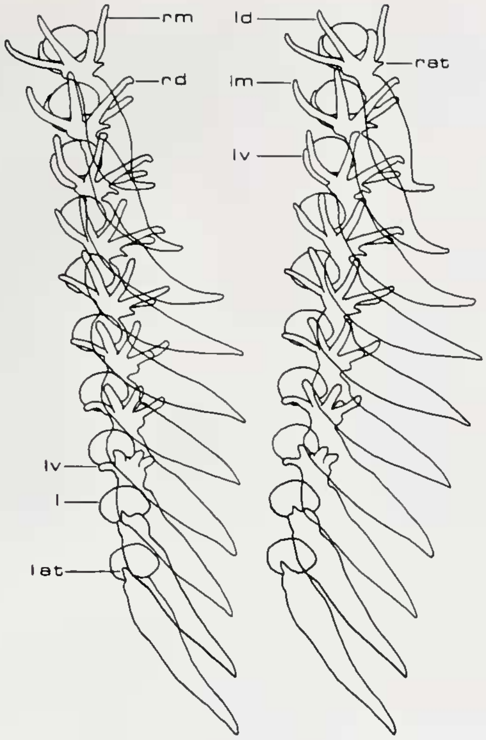

**Figure 3.** Tracings of *Clione* and *Limacina* from cine series with time intervals of 10 ms between frames and covering the 100 ms interval from one frame (10 ms) prior to the first sign of response to the prey through the initial grasping of the shell. The sequence has been plotted twice with a 7° shift in the y-axis. When viewed with a stereoscopic viewer or with crossed eyes, the sequence will appear in 3-dimensions with time represented in the z-plane. Buccal cone labels: (ld)—left dorsal, (lm)—left median, (lv)—left ventral, (rd)—right dorsal, (rm)—right medial. Right (rat) and left (lat) anterior tentacles are also labelled.

cal cones is nearly as rapid. This would suggest that both expansion and withdrawal are active responses. Fast-strike prey acquisition is thus distinct from the hunting behavior described by Litvinova and Orlovsky (1985) in which *Clione* rapidly swim with the buccal cones held in an expanded state. The initial phase of hunting behavior presumably involves similar mouth opening and buccal cone inflation.

The low success rate in triggering a fast-strike under laboratory conditions suggests that the fast-strike response has a high threshold for activation. Lowering of this threshold could result in behavior that is more disposed toward feeding, such as hunting behavior. In this case, the difference between responses to prey during normal swimming and those during hunting behavior might be one of motivational state. This difference can best be illustrated by comparing buccal cone responses during hunting and during an unsuccessful fast-strike response. In the former, the buccal cones are held in an expanded position despite the lack of mechanical contact with the prey. In the latter case, lack of prey contact results in a rapid withdrawal of the buccal cones and a return to normal swimming behavior. In hunting behavior, therefore, buccal cone withdrawal must be suppressed, even in the absence of direct mechanical contact with prey.

The nature of the trigger underlying the change in behavioral state, from hunting to fast-strike, is not known. It may, however, involve serotonergic input to the feeding system, because bath application or hemocoel injection of serotonin can trigger behavioral responses similar to those of hunting behavior; *i.e.*, the responses can be evoked although the animal has not been exposed to prey or prey extracts (Kabotyanski and Sakharov, 1988). The external stimulus for a switch to hunting behavior presumably involves chemosensory input because *Limacina* extracts, or proximity to feeding *Clione*, can initiate hunting behavior (Litvinova and Orlovsky, 1985).

Inflation of the buccal cones is remarkable for its great speed. Expansion is associated with a decrease in head and neck diameter, suggesting that increased hemocoelic pressure is associated with buccal cone inflation. Arshavsky *et al.* (1990) have shown that heart rate in *Clione* increases during hunting behavior, further supporting the idea that feeding responses are associated with increases in hemocoelic pressure. Pressure changes can be localized in the head as a muscular diaphragm separates head and body hemocoels. The diaphragm surrounds the anterior aorta and may act as a physiological valve further regulating blood flow to the hemocoel in the head (Lalli, 1967).

With buccal cones protruded, the *Clione* appear much like small squid. This led Wagner (1885) and Pelseneer (1885) to consider the possibility of homology between *Clione* buccal cones and squid tentacles. However, embryonic origins and innervation patterns demonstrate that they are not homologous (see Lalli and Gilmer, 1989, for a discussion of pteropod systematics and affinities). The mechanisms by which the two types of tentacles move to grasp their prey are quite distinct. Kier demonstrated that cephalopod tentacles are muscular hydrostats (Kier, 1982, 1987, 1988; Smith and Kier, 1989). Muscular hydrostats are readily distinguishable from hydrostatic skeletons that use a hydraulic mechanism in that their volumes are made up almost entirely of muscular tissue. Therefore, although they can undergo extensive changes in shape, muscular hydrostats do not substantially change volume. Hydraulic hydrostatic skeletons, in contrast, are fluid-filled cavities surrounded by muscular or fibrous tissues that resist the hydrostatic pressure within (Smith and Kier, 1989).

No clear differences are found when the speed of tentacle protractions in muscular hydrostats is compared with that of the hydraulic system of *Clione,* because the range of protraction speeds found in muscular hydrostat systems is very wide. For example, each of the 19 pairs of digital tentacles of *Nautilus* consists of an extensible, muscular,

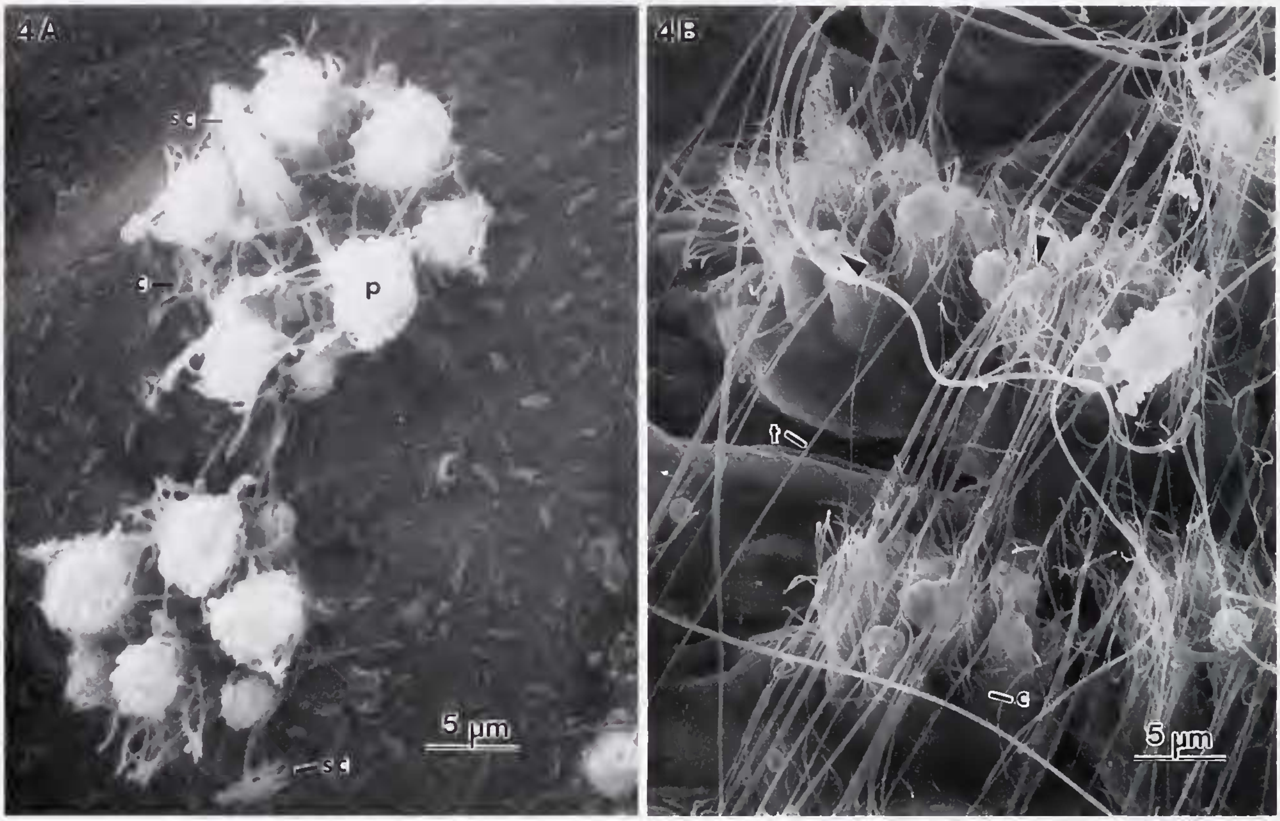

**Figure 4.** (A) Enlarged view of a part of one of the partially protruded buccal cones shown in Figure 1B. The head of each papilla (p) in the rosettes is studded with bumps. Motile cilia (c) project from the shaft of each papilla, whereas tufts of cilia (sc) project from the centers of rosettes, or less commonly are isolated from the rosettes. (B) Similar view of a region on a buccal cone of a different specimen, which was allowed to adhere to a *Limacina* shell and was fixed while grasping the prey. Dense mats of thread-like structures (t) can be seen on the adherent surfaces of buccal cones. Some appear to originate from the tips of capitulate papillae (arrows).

adhesive cirrus enclosed in a protective sheath. Protrusion of the cirrus from the tip of its sheath, which is necessary for it to grasp prey, requires 5–10 s or longer (Kier, 1987). At the opposite extreme, the tentacles of squid elongate fully in 15 to 30 ms (Keir, 1982, 1985).

The buccal cones of *Clione* can be protruded in less than 100 ms, and this performance is best appreciated when compared to other fast invertebrate prey capture behaviors that have been subjected to cine analysis. For example, prey seizure in the opisthobranch mollusk *Navanax* occurs in 380 ms; this is a muscular phenomenon involving a pharyngeal lunge followed by lip closure around the prey (Susswein *et al.*, 1984; Susswein and Achituv, 1987). Prey acquisition behaviors involving the movement of body parts that are supported by hard skeletal elements can be much faster; *e.g.*, the strike of the second thoracic appendages of stomatopod crustaceans occurs in 4–8 ms (Burrows, 1969).

Other gastropods can strike rapidly. In particular, the proboscides of toxoglossans, which contain poisonous, dart-like radular teeth, are potentially as rapid as the *Clione* buccal cone system. Predatory strikes have been described and photographed in a turrid, *Ophiodermella inermis* (Shimek and Kohn, 1981), and in *Conus* (Nybakken, 1967). The proboscis of *Conus* is protruded as a hydrostatic skeleton (Greene and Kohn, 1989), but the speed with which these strikes occur has not been analyzed by high speed cine or video.

Whereas some gymnosomatous pteropods do apprehend their prey with suction cups, somewhat like coleoidean cephalopods (Lalli and Gilmer, 1989; Kier and Smith, 1990), the adhesiveness of the buccal cones of *Clione* resembles that of the digital tentacles of *Nautilus*. The digital tentacles grip prey by means of ridges on the cirri that protrude from the tips of the sheaths that form the bases of the tentacles (Fukuda, 1987; Kier, 1987). In both *Nautilus* and *Clione*, the adhesive structures are ensheathed when not in use. In both cases, a question remains: to what degree are the prey simply gripped, and to what extent do the tentacles adhere? Fukuda (1987) suggested that the ensheathing of the cirri in *Nautilus* might serve to save mucus.

Apprehension of the prey by *Clione* may be partly by chemical adhesion and partly by the physical gripping of the *Limacina* shell by the enclosing buccal tentacles. The capitula of the papillae on the buccal tentacles might be thrust through the boundary layer of water, covering the hydrophobic surface of the *Limacina* shell and providing the means of attachment to, or gripping of the shell, just like the beaded gloves used by soccer goalies and football wide receivers aid in gripping the wetted, hydrophobic surfaces of footballs. In both cases, the bumps aid in adhesion; they penetrate the boundary layer of water, eliminating this weak boundary layer by driving it into the spaces between the bumps (Waite, 1987).

Because the buccal tentacles appear to be chemically adhesive and yet can detach to manipulate the shell of the prey so that the opening is aligned with the *Clione* mouth, the possibility that both adhesive and releasing chemicals are secreted must be considered (Hermans, 1983). Examination of the ultrastructure of the buccal cones and their secretions, as well as analyses of the control of feeding behavior, will help answer this and other questions about prey acquisition in *Clione*.

## Acknowledgments

We thank Dr. Tigran Norekian for translating Litvinova and Orlovsky (1985), Ms. Michelle Lagro for preparing specimens of *Clione* for electron microscopy, Prof. A. O. D. Willows of Friday Harbor Laboratories for space and equipment, Prof. R. Strathmann for use of his cine camera and the macro lens and video equipment, Dr. Tom Schroeder for instruction in SEM, also Mr. W. Sharp for instruction in EM and for the use of the Biological Electron Microscope Facility at Arizona State University, Mr. Chaz. Kazelik for help with the PC3D stereoscopic imaging program, Drs. Claudia Milis and Norm McLean for collecting and shipping specimens, and several other friends, colleagues, staff, and family at the Friday Harbor Labs for help in collecting specimens and for many other kindnesses. Thanks also to Sarah Cohen for suggesting the use of "Super Glue." Our perspective on the potential similarities between the strikes of toxoglossans and *Clione* has benefitted from discussions with Drs. Ron Shimek, Matt James, and Ed Smith.

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